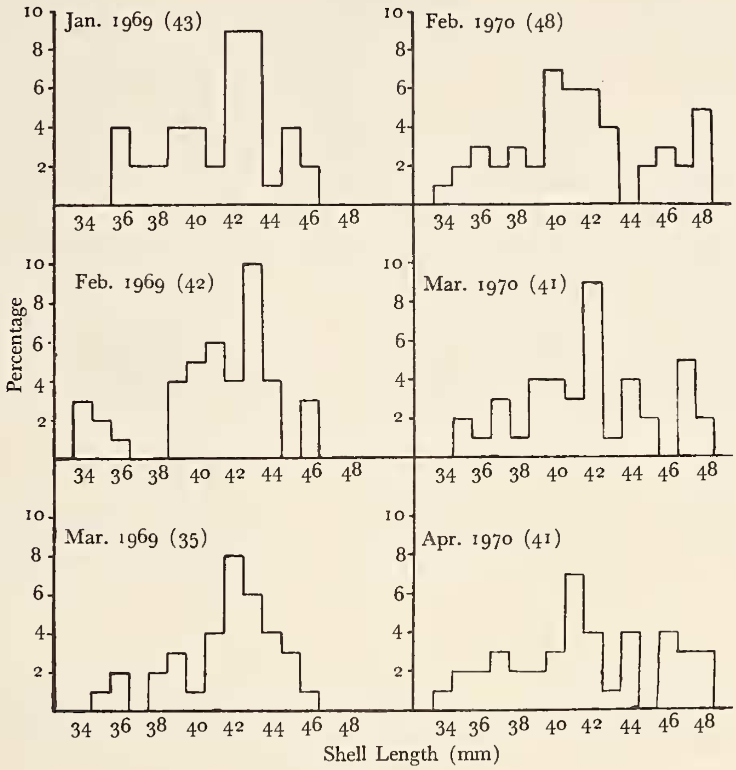


Figure 12

Frequencies of shell length in experimental samples measured in January-March, 1969 and February-April, 1970 to estimate growth

The Fishery: The cockles were collected by hand by women and children mostly. The latter usually went by dugout canoe to a mangrove area near their village and collected while the tide was low or for a period of about 2 to 4 hours. Average collecting rate 8.5 kg per hour (Table I). The cockles were used for subsistence, but any excess collected was commonly put in a small palm-frond house ("piangua house") between tides and so kept alive until needed. Some of these were taken to market.

A total of about 36 tons of mangrove cockles appeared in market records at Buenaventura in 1971. Month to month quantities were appreciably different (Figure 6). An additional 37 tons were recorded of road transport from Buenaventura to inland towns in Government fisheries statistics for 1971. At Tumaco, the second Pacific port of Colombia, an export of 44 tons to Ecuador was recorded. Market records were not obtained for this city but were reported to exceed those of Buenaventura. It may be concluded from these reports that about 150 tons of cockles were marketed in 1971. It is likely that a similar quantity was used in subsistence by coastal villagers.

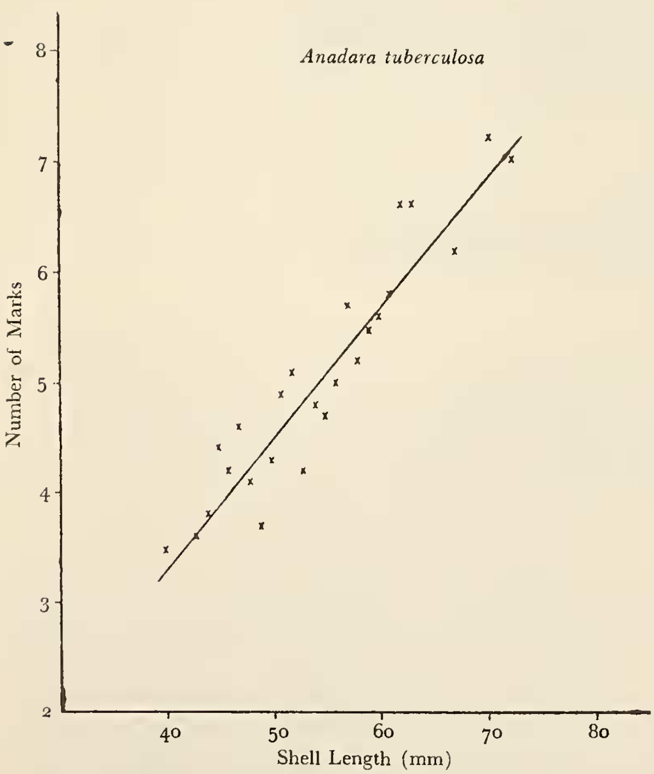
The keeping quality of the mangrove cockle and its ease of handling made for a food product in fairly steady supply. An experiment on holding live cockles out of water at usual temperatures of about 30°C showed that spoilage was not apparent in any of them up to 7 days, but they were rarely kept for more than 2 days by market vendors. Most were sold in the shell but some were cooked and the meats strung by the dozen on thin sticks of bamboo. Prices were low at about 3 US cents for a dozen in 1971.

Table 1

Collecting rates of mangrove cockles by individual fishermen from the Pacific coast of Colombia in 1972

Locality	Date	Total number collected	Hours collecting	Total weight kg	Rate kg/hr	Time required to collect 1 cockle sec.
Timbiquí	15 May	74	1	3	3	49
Timbiquí	15 May	21[3]	1[3]	1[3]	1[3]	172[3]
Bazán	16 May	192	2	—	—	37
Bazán	16 May	312	4	18	9	46
Bazán	16 May	264	4	16	4	54
Bazán	16 May	204	4	13	3.3	70
Bazán	16 May	1308	4	69	18.5	11
Bazán	16 May	1080	4	65	16.3	14
Bazán	27 June	65	¼	—	—	15
Bazán	27 June	137	½	—	—	13
Bazán	27 June	61	½	—	—	30
Averages					8.5	34

[3]Not included in averages



ECOLOGICAL CONSIDERATIONS

Cockles were found among mangrove roots intertidally, mostly buried in the soft mud and when not previously disturbed were attached by a byssus to mangrove rootlets, etc. Their distribution among the mangrove swamps appeared to be irregular with aggregations or areas of relative abundance, many of which were known to fishermen from fishing experience. An inexperienced collector could obtain only a fraction of the total amount available in an area.

When free in an aquarium, the cockles could move or burrow into the mud by siphonal jets of water and mud induced by rapid opening and closing of the shells. The cockles lay for long periods without moving, and when occasionally found at the surface of the mud in the field they were filtering actively with the shell slightly open. The cockles were always in the shade of mangroves, and temperatures in the mud varied from 26.0° to 37.5°C according to the time of day and the amount of sunshine

(← adjacent column)

Figure 13

Number of marks on the resilium at each length of shell of *Anadara tuberculosa*

(Records from a Ryan Thermograph over a 3 week period in October, 1972). Salinities were estuarine varying from 15 to 23‰ in the observations made.

Some of the macrofauna present with the cockles in the mangrove ecosystem were: the tree-climbing crab, *Goniopsis gaudichaudi;* species of alphaeid shrimps that made loud snapping noises continuously while the tide was out; other caridean shrimps, mostly palaemonids; juvenile penaeid shrimps; hermit crabs of several genera and species; some small fishes, and at least 3 species of littoral gastropods.

During one afternoon of dredging in the large open water estuary of Buenaventura near Corvinero, some specimens of post-larval cockles 1–2 mm in length (similar to those described by PATHANSALI, 1963) were obtained at depths of 3–5 m. Cockles larger than this and up to a length of 30 mm were not seen in these investigations nor during this study.

DISCUSSION AND CONCLUSIONS

Although the quantity of cockles available for the total area was estimated at 1500 tons, it was unlikely that this amount could be harvested each year. It could be argued that since growth was slow between shell lengths of 30–66 mm (about 1 mm each month on the average) at least three years would be required for each animal to reach a commercial size of 66 mm. However, if survival of recruits were relatively constant each year, about ⅓ of the total

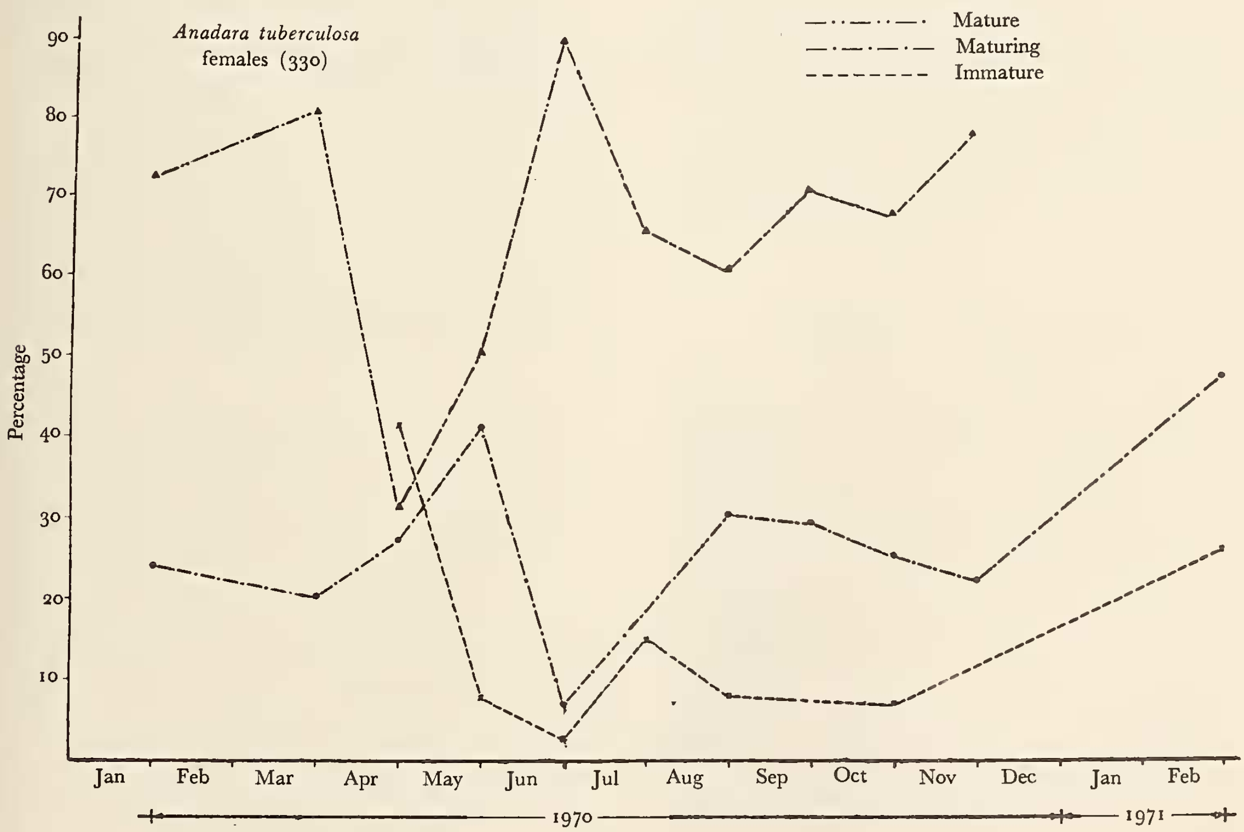


Figure 14

Percentages of immature, maturing and mature *Anadara tuberculosa* in monthly samples from January, 1970 to February, 1971 amount would reach commercial size. This amount or about 500 tons could be harvested each year without depleting the stock, if recruitment were relatively constant as premised.

If the fishery expanded, 500 tons could be harvested by 250 fishermen fishing 150 days a year at an average rate of 15 kg per day per fisherman. Several thousand people lived in villages along the coast and this number or more would be available if required.

Fresh meat weights would be about 18% of the total weight of cockles, but this would be somewhat reduced under cooking. However, the fresh meat weight of 500 tons would amount to only 90 tons. The present rate of exploitation seemed appropriate in view of the part played by the cockle in the subsistence of coastal peoples.

ACKNOWLEDGMENTS

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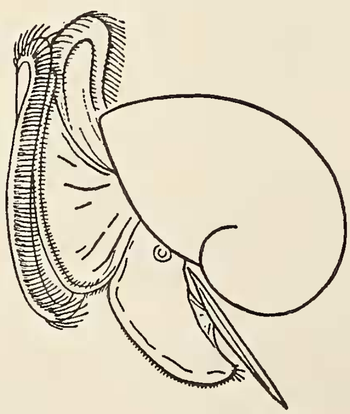

The Importance of Size in the Intertidal Distribution of *Littorina scutulata*

(Gastropoda: Prosobranchia)

BY

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(8 Text figures)

INTRODUCTION

The spatial partitioning of a habitat by the different growth stages of an organism has been observed frequently in many animal species; in marine intertidal gastropods, this partitioning is often in the form of a gradient in body size along a vertical transect of the shore. Such size gradients appear in chitons (Boyle, 1970) and in snails (North, 1954; Paine, 1969; Sutherland, 1970; Vermeij, 1970; Haven, 1971), but the factors causing such distributions generally lack thorough understanding. The importance of many of the size gradients has yet to be established in terms of the mode of life and the habitat of the species.

The purpose of this study is to investigate the characteristics of, and the factors influencing, the size gradients of *Littorina scutulata* Gould, 1849, a common upper littoral gastropod of the west coast of North America. North (1954) and Bock & Johnson (1967) have presented limited data concerning size-class distribution in *L. scutulata* in the course of their studies, and have suggested possible environmental factors which could limit the vertical range of the species. However, information resulting from their works is insufficient for determining the exact nature of the size gradient of *L. scutulata*. Additional information, so as to make a detailed analysis of size-class distribution possible, is one object of this investigation.

Previous studies have often assumed that physical stresses at the limits of a species' range are the principal cause of vertical zonation. Conditions such as desiccation, high temperatures, osmotic stress, and wave shock, can form gradients of mortality in the marine intertidal zone, and may be factors in a species' size-class distribution through differential mortality of one size group relative to another over the entire vertical range of that species. In the case of mobile animals such as *Littorina scutulata*, a size gradient may also result from the active migration of one size group relative to another. It is the further intent of this study to test various size groups of *L. scutulata* for their relative abilities to withstand environmental stress conditions and for differences in behavior which would reveal migrational tendencies. The results will be interpreted with regard to observations on the size-class distribution of the species.

MATERIALS AND METHODS

Transects: This study was carried out during the months of April and May on Bodega Head, Sonoma County, California. In order to determine the distribution of *Littorina scutulata*, information was collected along two transects spanning the intertidal zone. Region 1 (Figure 1) occupied a position on the southwest shore of the peninsula, near Windmill Cove, and represented a moderately steep slope which received fairly heavy wave action from the open ocean. Region 2 (Figure 1) lay to the south of the Bodega Harbor entrance on a relatively gentle slope, and was sheltered from heavy wave action. At both locales, the rocky shore consisted of extremely rugged diorite granite and extended uninterrupted through the entire intertidal sampling area. Counts were conducted at each region from about mean lower low water (MLLW) to beyond the limits of high-water splash. At intervals of 0.1524 m above MLLW, all *L. scutulata* present in 5 randomly placed 15 × 15 cm quadrats were counted and measured. The maximum linear shell dimension or height (the distance from the apex of the shell to the farthest point on the outer lip), measured to the nearest millimeter, served as a basis for defining the size of the littorinids (Figure 2).

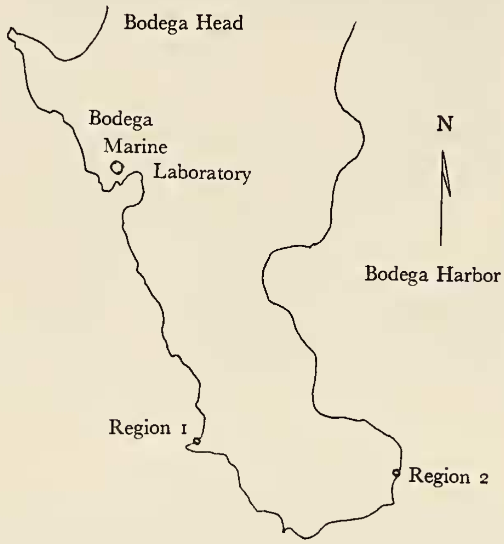

Figure 1

Map of Bodega Head, showing the approximate locations of the two transects

Physical Factors: Tolerances to environmental conditions that might produce stress on *Littorina scutulata* in the field were investigated in the laboratory, to determine if size differences could allow exploitation of different parts of an intertidal gradient. The following experiments involved the measurement of relative mortality of various sizes of snails to conditions of physical stress.

Tests of the osmotic tolerances of *Littorina scutulata* involved exposing them to freshwater and hypersaline solutions. Groups of *L. scutulata* of three size classes (3–4; 6–8; 10–13 mm) remained immersed in (uncirculated) fresh tap water at 18° C. Samples (5 of each size class) were removed at given intervals, and survival was assessed 24 hours later, after returning the snails to sea water (18° C) for recovery. The same procedure was repeated for a hypersaline solution, using 200% artificial sea water ("Instant Ocean," Aquarium Systems, Inc.) at 18° C. As a control population, groups of *L. scutulata* also stayed submerged in normal sea water. Survival at the conclusion of these experiments was based on the ability of the test organisms to resume normal locomotion, which included the ability to climb vertical glass surfaces. Snails incapable of normal locomotion, even if capable of some movement, were considered dead since, in the field, they would be unable to carry out necessary life functions.

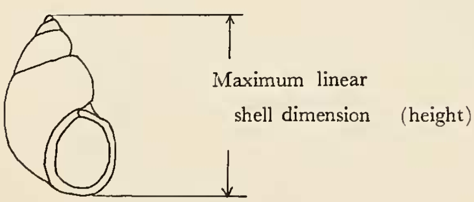

Figure 2

Littorina scutulata, showing the method of measuring shell size

Investigations of desiccation tolerances and rates compared 4 size classes of *Littorina scutulata* (6, 9, 12, 15 mm ± 0.2 mm). Individual test specimens remained at the bottom of plastic vials; moving air of fairly constant velocity and temperature (19° C) crossed the open ends of the vials. Periodic weighing of the vials allowed calculation of desiccation rates. At the termination of this experiment, survival percentages were noted, and dry weights were subsequently obtained in order to determine total initial body water (wet gross weight – dry gross weight).

Experiments on the thermal tolerances of different size classes of *Littorina scutulata* during immersion in sea water compared survival of snails in a procedure similar to that used by FRAENKEL (1968) and by WOLCOTT (1973) on intertidal snails, in which each individual received a similar heat dosage. Fifteen snails (5 from each of 3 size classes: 3–4; 6–8; 10–13 mm) remained in a beaker of sea water at the desired test temperature for 15 minutes; the beaker itself occupied a position in a water bath of the same test temperature. Survival was assessed after a 24 hours recovery period in running sea water (14° C), using the same criteria as in previous experiments.

In analyzing the relative effects of wave action, various sizes of *Littorina scutulata* participated in trials which used a technique similar to that of NORTH (1954). Test specimens of four size classes (3–4; 6–7; 9–11; 12–13 mm) were positioned in a glass tube (14 mm inside diameter), and after the snails had begun moving about, the tube was gently filled with sea water at 11° C. A current of known velocity (calculated by measuring the volume of water flowing through the tube in a given time) then passed through the tube and the abilities of the snails to remain attached for ten seconds were noted. Snails were tested one at a time, and mucous trails were cleaned from the glass before each trial to prevent possible interactions from one test to the next. Trials, using 10 individuals from each size class, involved water current velocities of 0.8, 2.2, and 3.0 meters per second.

Behavior: Migrational tendencies and the role of behavior in segregating the size classes of *Littorina scutulata* were studied in the field at region 1. Fifty large snails (10–12 mm) and 50 small snails (3–4 mm) were placed on a bare, horizontal ledge, 1.68 m above MLLW, and an equal number of snails on a ledge 3.05 m above MLLW. (Red and yellow enamel paint labeled test specimens.) Vertical movements and the type of habitats selected by individual snails were periodically noted. Observations in the laboratory supplemented the information on the behavior of *L. scutulata* obtained in the field.

RESULTS

Transects: The transects of both region 1 and region 2 ran from 0.9 m to 4.1 m above MLLW, and included zones of barnacles (1–2 m above MLLW), *Pelvetiopsis limitata* Gardner, 1910 (2–3 m above MLLW), and bare rock with microscopic algal forms (3–4 m above MLLW). Region 2, however, supported much more densely populated levels of barnacles and *P. limitata*. Small clusters of mussels occupied scattered sites between 1.2 and 2.1 m above MLLW at both locales.

The shell sizes of *Littorina scutulata* collected along the 2 transects covered a range from 1 to 12 mm, with the majority of snails falling in the two- and three-millimeter size classes (Figure 3). The vertical distributions of the species (Figure 4) show a total range from 1.07 m to 3.81 or 3.96 m above MLLW, with a peak in population density at about 2.1 or 2.3 m; yet, in relation to smaller snails, snails with shells of sizes 5 to 12 mm occupy a narrower zone (region 1: 2.13–3.35 m; region 2: 1.83–3.35 m above MLLW). The smaller snails (1–3 mm) indicate additional zonation by size, with the majority of two-millimeter snails occurring at levels above the majority of one-milli-

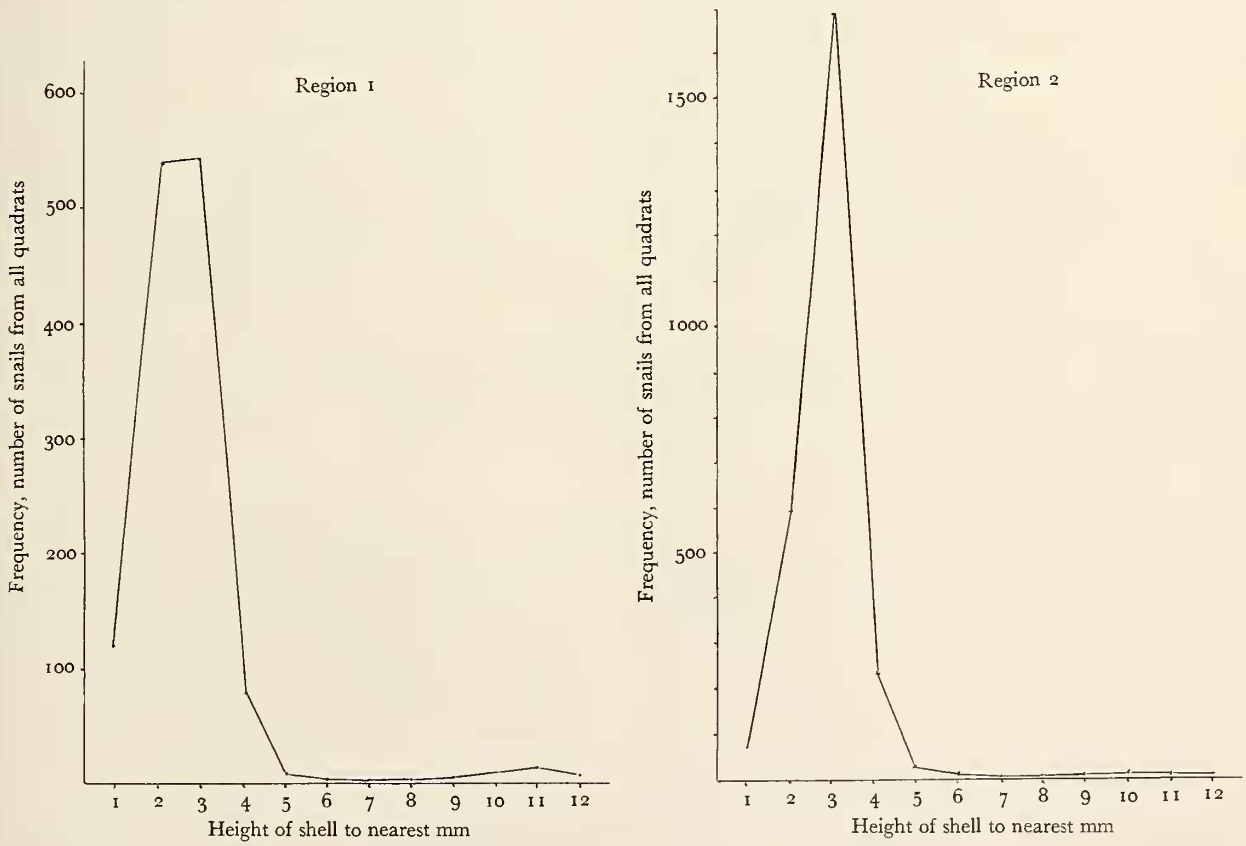

Figure 3

Size frequencies of *Littorina scutulata*

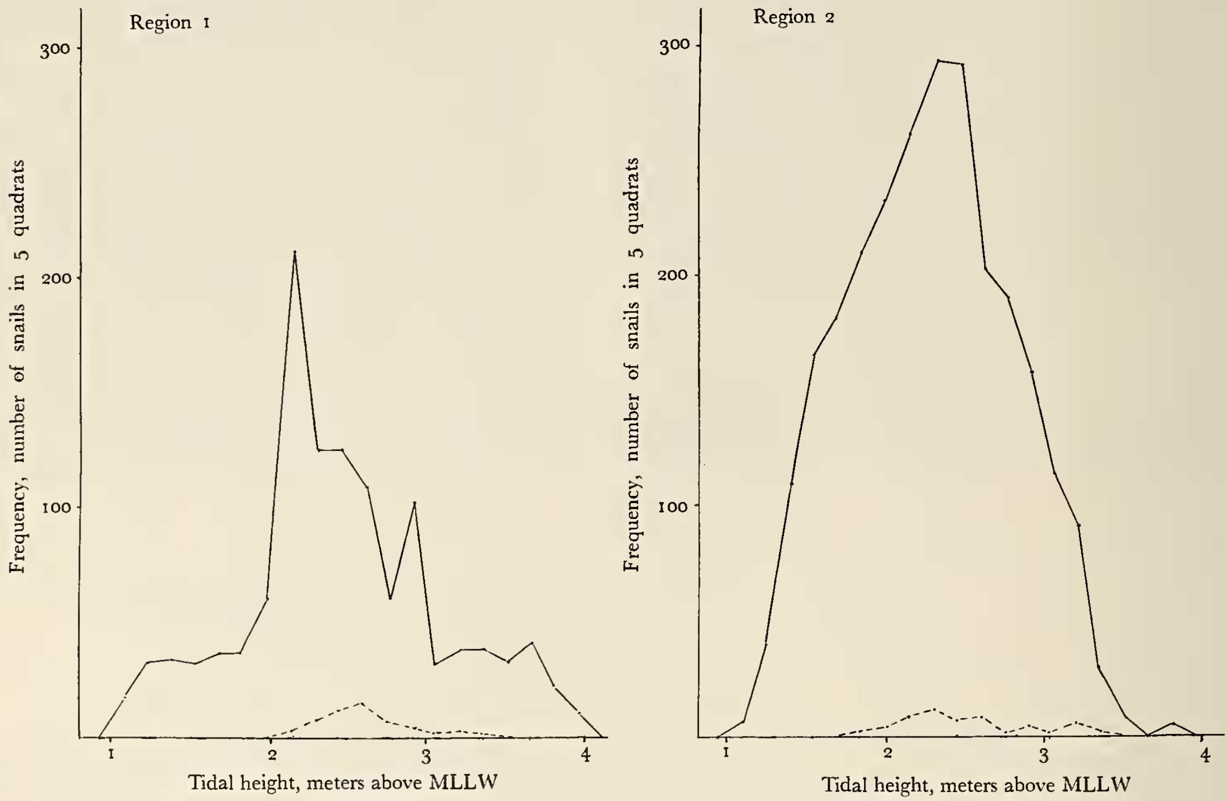

Figure 4

Vertical distribution of two size classes of *Littorina scutulata*
——— 1 - 4 mm snails, measured to nearest mm
– – – – 5 - 12 mm snails, measured to nearest mm

meter snails, and the majority of three-millimeter snails occurring at levels above the majority of two-millimeter snails (Figure 5). The small *L. scutulata,* nevertheless, had much broader distributions than the larger snails (5–12 mm).

Physical Factors: *Littorina scutulata* of all sizes can survive submersion in normal sea water for over 10 days; 70 snails of various sizes emerged unaffected after this length of time in the laboratory. However, tolerances to osmotically stressful solutions are higher for large-size classes of *L. scutulata.* In laboratory determinations of tolerance to freshwater (as rain or freshwater seepage), median lethal limits (the earliest times for which more than half of the sample is killed) are reached first by 3–4 mm snails and second by 6–8 mm snails, while 10–13 mm snails fail to die in sufficient numbers during 120 hours of immersion (Table 1). Many of the dead snails had burst from the openings of their shells, presumably due to osmotic stress. Large snails also withstand hypersaline solutions (as in cases of evaporated sea water) better than small snails. Table 1 also presents results and lethal limits of snails exposed to 200% sea water.

Typical patterns of desiccation for 4 size classes of *Littorina scutulata* appear in Figure 6. The high initial rate of water loss occurs during the period when evaporation of water from body and shell surfaces is the rate-limiting factor. The subsequent lower rate indicates loss of water

Table 1

Tolerance of three size classes of *Littorina scutulata* to immersion in fresh water and to immersion in 200% sea water
Italicized values denote lethal limits; sample n=5

Time Immersed (hours)	% Mortality in Fresh Water			% Mortality in 200% Sea Water		
	3-4 mm	6-8 mm	10-13 mm	3-4 mm	6-8 mm	10-13 mm
42	0	0	0	0	0	0
62	0	0	0	*60*	*60*	0
76	40	40	0	80	60	*60*
89	*60*	40	0	100	100	60
100	60	*60*	0	100	100	100
120	100	60	40	100	100	100

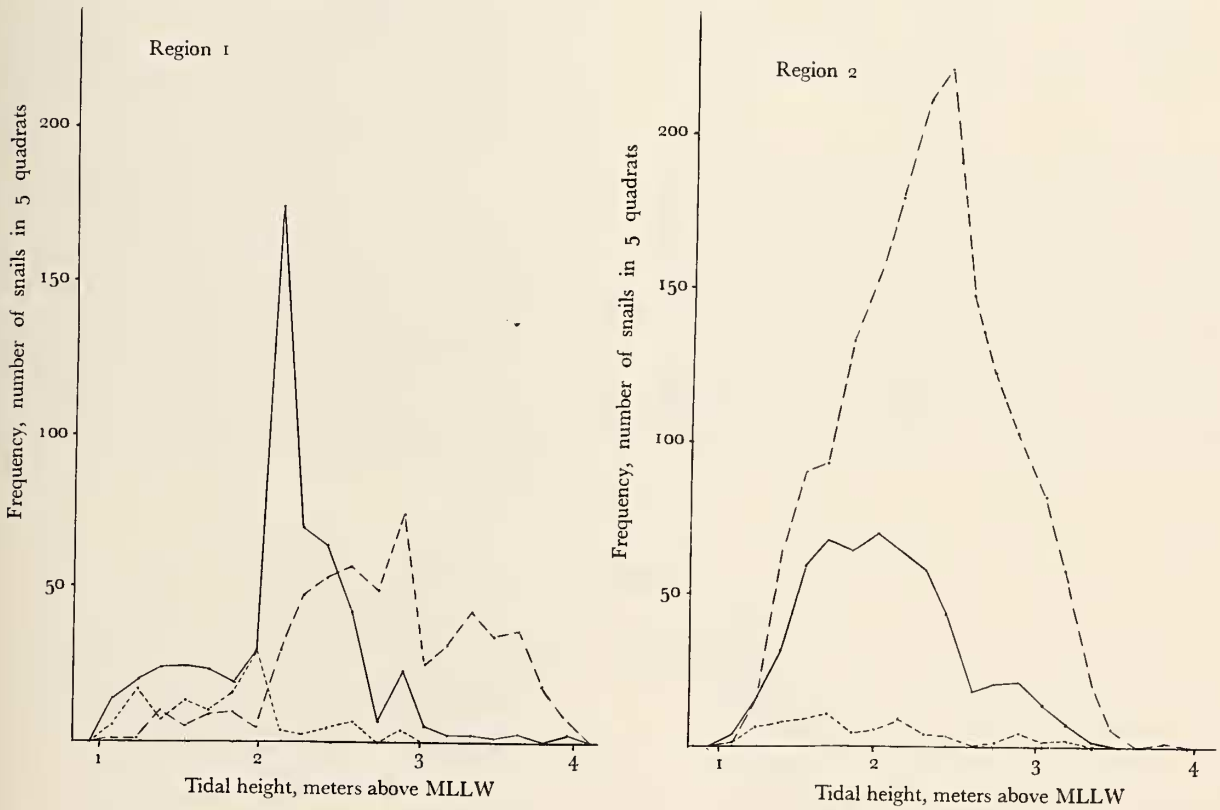

Figure 5

Vertical distribution of *Littorina scutulata,* shell sizes 1-3 mm
- - - - - - 1 mm snails
——— 2 mm snails
– – – – 3 mm snails

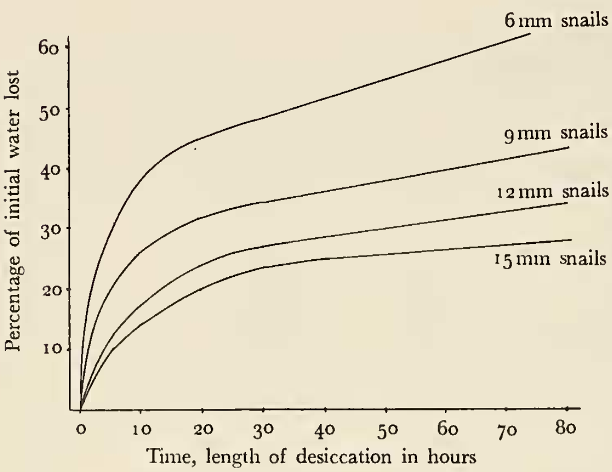

Figure 6

Typical patterns of desiccation for 4 size classes of *Littorina scutulata*

which has diffused from underlying body tissues. Determination of desiccation rates was based on this diffusion-limited period of desiccation, and the results are presented in Table 2. Large snails (15 ± 0.2 mm) had significantly lower desiccation rates than smaller snails, and of 20 snails tested, the only mortality of *L. scutulata* after 96 hours of desiccation occurred in one of the smallest snails (6.0 mm).

In the laboratory, thermal tolerance during immersion in sea water seems to be independent of size; no statistically significant intraspecific differences appeared. Lethal limits (the lowest temperature killing more than half of the sample tested) occur at 45° C for all tested size classes, while mortality is 100% at 46° C. No deaths were noted below 44° C.

The effectiveness of water currents in removing snails from surfaces is greatest for small *Littorina scutulata*. In laboratory investigations, large snails withstand higher water current velocities as shown in Table 3.

Behavior: Observations in the laboratory on behavior of various sizes of *Littorina scutulata* fail to reveal significant differences in (vertical) migrational tendencies. Regardless of size, snails demonstrate a negative geotactic response by climbing out of the water when placed in an aquarium (to heights as far as 60 cm above the water surface—the top edge of the tank). Apparently, they would climb up as far as the glass surface was kept moist by water from the snails' bodies.

In the field, however, large *Littorina scutulata* (10–12 mm) exhibited considerably greater migrational behavior than small snails (3–4 mm). Vertical movements of snails, large and small, for a period of over 2 days, are shown for test specimens placed at 1.68 m (Figure 7) and 3.05 m above MLLW (Figure 8). In both instances, the average position of the large snails was between 2.75 and 3.00 m at the termination of observations in the field, and there was no statistically significant difference in the means. Of the large snails recovered, 82% had taken positions in large crevices in the rocks, while the remaining ones were found on *Pelvetiopsis limitata*. In contrast, 86% of the small *L. scutulata* placed low had crawled in or about clusters of barnacles; 60% of the small snails placed high had moved into large crevices, but 36% took positions in

Table 2

Dessication rates for four size classes of *Littorina scutulata*
Means ± one standard deviation (n=5)

Size Class (ht)	Range of wet wt. (grams)	Range of dry wt. (grams)	Dessication Rates (% total water lost/hr.)
6 ± 0.2 mm	0.033-0.046	0.018-0.032	0.370 ± 0.184
9	0.117-0.175	0.074-0.113	0.130 ± 0.043
12	0.290-0.415	0.197-0.258	0.136 ± 0.042
15	0.600-0.767	0.454-0.644	0.099 ± 0.032

Student t-test: 9mm, 12mm rates < 6mm rate, $P < 0.05$
15mm rate < 6mm, 9mm, 12mm, $P < 0.001$
difference not significant between 9mm and 12mm rates